

A NEW PLIOSAUR FROM THE BAJOCIAN OF THE NEUQUEN BASIN, ARGENTINA

by ZULMA GASPARINI

ABSTRACT. A new pliosaur with a spatulate symphysis is described as *Maresaurus coccai* gen. et sp. nov. The holotype is from the upper levels of the Los Molles Formation (Lower Bajocian, Middle Jurassic) of the southern Neuquén Basin, central-western Argentina. *Maresaurus coccai* shares with *Simolestes* such synapomorphies as the absence of a dorso-medial foramen, lack of anterior interpterygoid vacuity, and fewer than 26 alveoli in the dentary. The autapomorphies of *M. coccai* are the strong flanges formed by the premaxillary and maxillary, the expanded and elevated pterygoid wings, a diastema between the eighth and ninth mandibular alveoli and the hypertrophied teeth (caniniforms) which are densely striated and without carinae or smooth faces. The record of Bajocian plesiosaurs is restricted to *Simolestes keileni* from the Upper Bajocian of France and *M. coccai* from the Lower Bajocian of the Neuquén Basin. The latter is associated with other marine reptiles, mainly ichthyosaurs, coeval with greater diversity in the invertebrate fauna, in an offshore deposit dominated by pelagic sedimentation.

MOST Jurassic Pliosauroida (*sensu* Brown 1981) have been found in Europe, mainly in the Lias of England and Germany (Fraas 1910; Taylor 1992*a*, 1992*b*), in the Lower and Middle Oxford Clay (Middle–Upper Callovian) of England (Andrews 1913; Tarlo 1960; Brown 1981; Martill 1991) and in the Oxfordian and Kimmeridgian of England and France (Taylor and Benton 1986; Bardet 1992, 1993; Mazin *et al.* in press). Outside the European Tethys region, the record of Jurassic pliosauroids is poor (Persson 1963; Gasparini 1985, 1992; Bardet 1992; Gasparini and Fernández 1996, in press). However, after the Lias and before the Callovian, pliosaur records are particularly sparse. Hitherto, only a pliosaurid from the Upper Bajocian of Lorraine, France (*Simolestes keileni* Godefroit, 1994), and a supposed rhomaleosaurid (*sensu* Kuhn 1961) from the Middle Jurassic of the Sichuan Basin, China (*Yuzhoupliosaurus chengjiangensis* Zhang, 1985) have been published. Here, I describe a new pliosaurid from the Neuquén Basin.

Pliosauridae (*sensu* Brown 1981) with spatulate snouts are known from: the Hettangian of England, *Rhomaleosaurus megacephalus* (Stutchbury, 1846) (see Cruickshank 1994), and *Euryceleidus arcuatus* (Owen 1840); the Lower Toarcian of England, *Rhomaleosaurus thorntoni* (Andrews, 1922), *R. zetlandicus* (Phillips in Anon. 1854, *fide* Taylor 1992*a*, 1992*b*), *R. propinquus* (Watson, 1910) and *R. cramptoni* (Carte and Baily, 1863); and the Upper Toarcian of Holzmaden, *Rhomaleosaurus victor* (Fraas, 1910). Recently, Cruickshank (1994) noted that *R. zetlandicus*, *R. cramptoni* and *R. thorntoni* could represent a single species. Part of a postcranial skeleton found in the Upper Lias of the Sichuan Basin (*Bishanopliosaurus youngi* Dong, 1980) was also referred to a pliosaurid (Rhomaleosauridae *sensu* Kuhn 1961). Other pliosaurids with a spatulate symphysis are: *Simolestes keileni*, from the Upper Bajocian of France (Godefroit 1994); *Simolestes vorax* Andrews, 1909, from the Middle Callovian of England (Martill 1991) and from the Lower Callovian of Normandy (Bardet 1993) and the Calcaires Blancs du Poitou (Mazin *et al.* in press); *Simolestes* sp. from the Callovian of the Moscow Basin (Tarlo 1960); *Yuzhoupliosaurus chengjiangensis* Zhang, 1985 from the Middle Jurassic of the Sichuan Basin; and *Simolestes indicus* (Lydekker) (Bardet *et al.* 1991) from the Tithonian of Kachchh, India. *Simolestes nowackianus* von Huene, 1938, from the Oxfordian of Ethiopia, has been reinterpreted as a specimen of the teleosaurid crocodile *Machimosaurus* (Bardet and Hua in press). Bardet (1992), Taylor (1992*b*) and Godefroit (1994) have pointed out that the taxonomy of *Rhomaleosaurus* and other pliosauroids needs to be

reviewed. There were pliosaurids with a spatulate symphysis throughout the Jurassic across a wide sector of the Tethyan belt, but the new pliosaurid from the Lower Bajocian of the Neuquén Basin is the first record from the Eastern Pacific. The Early Jurassic pliosauroids with a spatulate symphysis were included within the family Rhomaleosauridae Kuhn, 1961 (Persson 1963), an invalid taxon (Brown 1981) because of the absence of unequivocal synapomorphies supporting it.

Early in 1988, the author undertook fieldwork in the area of Chacaico Sur (Sierra de Chacaico), Neuquén province, north-western Patagonia, accompanied by Dr Luis Spalletti, sedimentologist of the Instituto de Investigaciones Geológicas from the Universidad Nacional de La Plata, Messrs Sergio and Rafael Cocca, technicians of Museo Profesor Olsacher of Zapala, Neuquén, and local people. That fieldwork covered the upper section of the Los Molles Formation (Cuyo Group; Dellapé *et al.* 1978), referred to the Lower Bajocian (Spalletti *et al.* 1994). The Neuquén Basin is on the western margin of South America (Eastern Pacific), (32–41° S, 68–72° W). The top of the Los Molles Formation in the Chaciaco Sur area is composed of dark shales and marls with sandstone intercalations. This section, where the new pliosaurid was discovered, is interpreted as an offshore deposit dominated by pelagic sedimentation, with the sands, introduced by storm-induced orbital and gravitational flows (Spalletti *et al.* 1994).

SYSTEMATIC PALAEONTOLOGY

Superorder SAUROPTERYGIA Owen, 1860

Order PLESIOSAURIA de Blainville, 1835

Superfamily PLIOSAUROIDEA (Seeley, 1874) Welles, 1943

Family PLIOSAURIDAE Seeley, 1874

Genus MARESAURUS gen. nov.

Derivation of name. From *mare*, the Latin word for sea, and *sauros*, the Greek word for lizard.

Type species. *Maresaurus coccai* sp. nov.

Diagnosis. As for the type and only species.

Maresaurus coccai gen. et sp. nov.

Text-figures 1–4

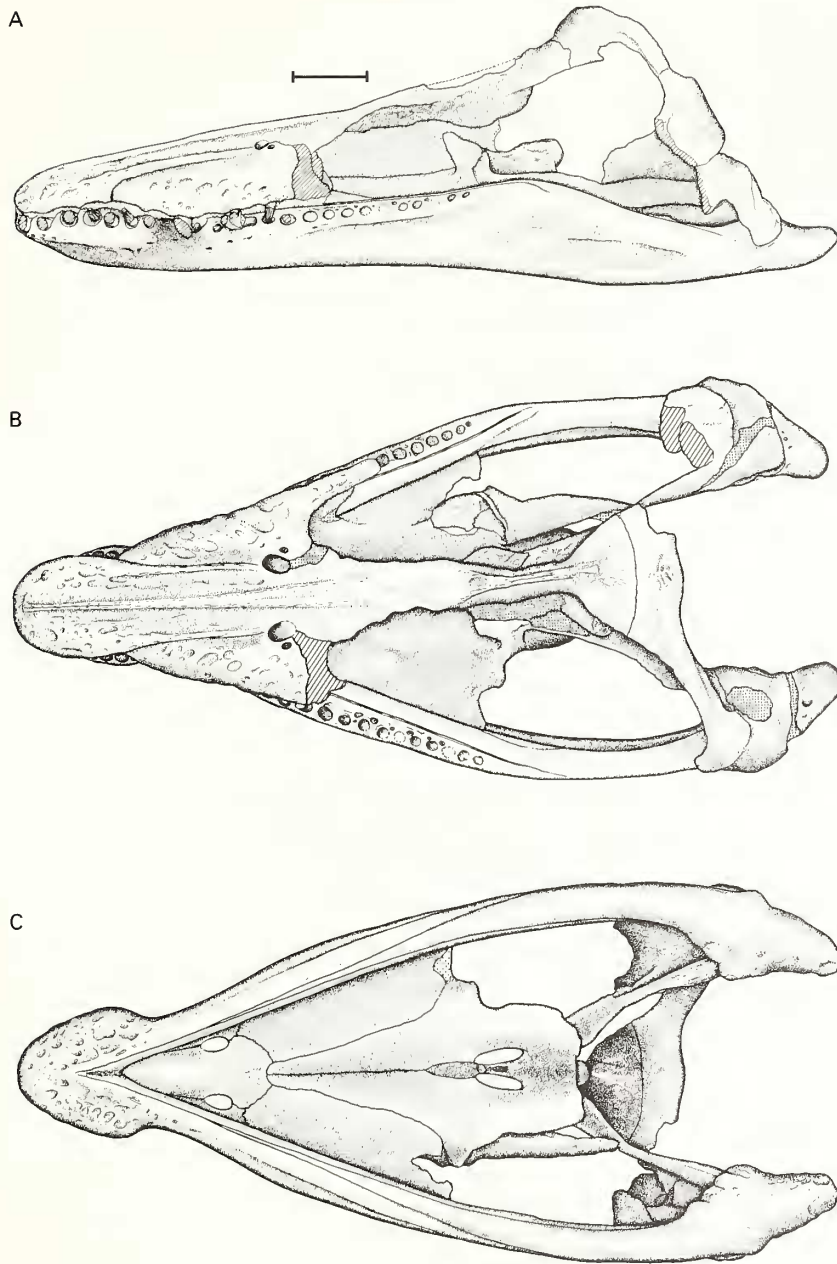
1993 *Simolestes* sp. Gasparini and Fernández, p. 107

Derivation of name. Dedicated to the brothers Sergio and Rafael Cocca, members of the Museo Prof. Olsacher of Zapala, and valuable collaborators in all the fieldwork related to the search for marine reptiles in the Neuquén Basin.

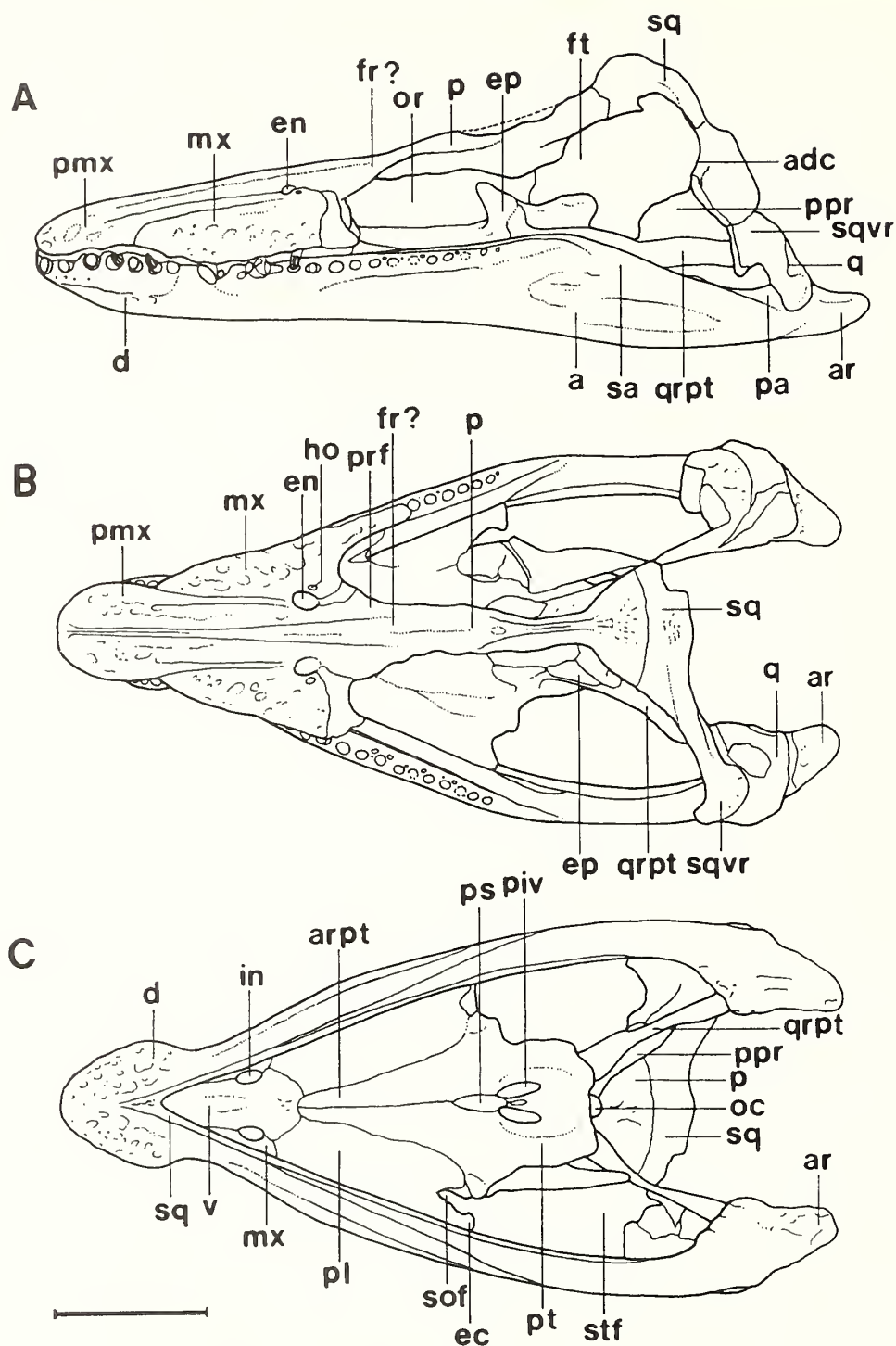
Holotype. Museo Prof. Olsacher, Zapala, Neuquén (MOZ 4386 V), articulated skull and mandible, fused atlas and axis, and the first cervical vertebrae.

Locality and horizon. Chacaico Sur, (39° 15' S, 70° 18' W), 70 km south-west of Zapala, Neuquén Province, Argentina (Spalletti *et al.* 1994); upper part of the Los Molles Formation, Cuyo Group (Dellapé *et al.* 1978; Leanza 1990; Riccardi and Gulisano 1990). The new pliosaurid comes from a level of dark shales and marls. Within the *Enileia giebeli*, *Enileia multiformis* subzone, Lower Bajocian, Middle Jurassic (Spalletti *et al.* 1994).

Diagnosis. Pliosaurid with spatulate symphysis incorporating six pairs of alveoli. Rostrum deep, with marked sagittal crest, formed by union of premaxillae, and two conspicuous parallel crests, formed by dorsal union of premaxillae and maxillae. Deep notch between premaxilla and maxilla, and marked anterior wave in maxilla incorporating six alveoli. External surface of the premaxillae and maxillae with deep cavities. No dorsomedial foramen in premaxillae. Posterior region of the



TEXT-FIG. 1. *Maresaurus coccai* gen. et sp. nov.; MOZ 4386 V; Lower Bajocian, Neuquén Basin, Argentina. A, lateral view; B, dorsal view; C, ventral view. Scale bar represents 100 mm.



TEXT-FIG. 2. *Maresaurus coccai* gen. et sp. nov.; MOZ 4386 V; Lower Bajocian, Neuquén Basin, Argentina. Scale bar represents 200 mm. For abbreviations see Appendix.

parietal wide, without enclosing posterior edge of skull and not extending below dorsal ramus of squamosal. Occipital condyle not exposed in dorsal view. No anterior interpterygoid vacuity. Very high pterygoid posterior wings. Parasphenoid not separating interpterygoid vacuities completely. Twenty-four teeth in dentary. Anisodonty. All the teeth with circular section, densely distributed non-dichotomized striae, and without carinae. Hypertrophied (caniniform of Tarlo 1960) teeth without smooth faces.

DESCRIPTION

Skull and mandible

The skull is sub-triangular in dorsal view, with a rather short and spatulate rostrum as in *Rhomaleosaurus* and *Simolestes*. In lateral view, the rostral height, the cranial height (which reaches its maximum in the squamosals), the notch between premaxillae and maxillae, and the strong maxillary wave are important features (Text-fig. 1). The medial sector between the external nares and the squamosals is damaged by erosion and compressional effects after fossilization, as the parietal crest was the only bony element exposed on the surface. Most dorsal cranial sutures are missing, and the temporal arches are lost. In contrast, the palate and the mandible are excellently preserved. The mandible is strongly attached to the skull and rostrum, in part due to the large, partly intermeshed teeth.

Premaxillae. The premaxillae, the lateral edges of which are anteriorly slightly convex, form the anterior part of the snout which is blunt-ended. In this anterior region, there are several hollows irregularly distributed and pores near the dentary margin. In the posterior part of the rostrum and above the maxillae, the premaxillae form a crest which, at the anterior edge of the external nares, bifurcates into two gentle domes which merge with the frontals or parietals. Unlike *Rhomaleosaurus* (Carte and Baily 1863; Taylor 1992b; Cruickshank 1994) and *Simolestes* (Andrews 1913), the contact between premaxillae and maxillae produces a strong crest which runs from the notch up to the anterior edge of the naris. Between the premaxillary-maxillary contact crests and the medial premaxillary crest there are two deep depressions, ornamented with irregularly distributed hollows in the anterior part, and tiny striae running anteroposteriorly (Text-fig. 1B). Unlike *Rhomaleosaurus*, *Maresaurus coccai* lacks a dorso-medial foramen above the premaxillae. Ventrally, the premaxillae are covered by the mandibular symphysis which is wider than the anterior edge of the snout. However, the alveoli of the functional teeth, five in each premaxilla, are exposed. The amount of dorsal extension of the premaxillae and their degree of participation in the narial margins, are unknown. As the medial crest of the premaxillae is damaged at the anterior edge of the external nares, the premaxillary domes are slightly depressed, and the frontal and prefrontal sector is partially eroded, it is impossible to ascertain whether the premaxillae were dorsally in contact with the frontals, or directly with the parietal (Text-fig. 1B). If the dorsal contact was with the parietal, the frontals would have remained laterally situated, as in *Rhomaleosaurus zetlandicus*. Unfortunately, details of this region are obscure in both *R. cramptoni* and in *Simolestes vorax*. In the latter, Andrews (1909, p. 427) pointed out that the premaxilla and frontal merge by the anterior edge of the orbits, but he later stated (Andrews 1913, p. 26) that the contact was made between the premaxillae and the parietal, with the frontals left outside. Following examination of the holotype (BMNH R3319), I concur with the latter opinion. In *Maresaurus coccai*, the frontals form the upper margin of the orbits and, in lateral view, they have deep furrows and crests where the postorbital arches, which are missing, were attached (Text-fig. 1A).

Maxillae. The maxillae are almost complete, especially the right one, the alveolar edge of which is preserved up to mid-orbit level. The lateral walls of the maxillae are high, and bear, as in many crocodiles, a marked anterior wave which comprises the first six alveoli (Text-figs 1A, 2A). In *Rhomaleosaurus thurstoni* and *Simolestes vorax*, this maxillary wave is less evident, probably as a result of flattening. The large oblong cavities which cross the maxillae from posterodorsally to anteroventrally are a remarkable peculiarity. Similar pronounced cavities are also present in *R. victor* and *R. cramptoni*. The similarity of the sculpture of *R. cramptoni* to that of some crocodiles was pointed out by Carte and Baily (1863). The lateral contact between maxillae and premaxillae forms a strong crest starting with a marked marginal notch where a hypertrophied mandibular tooth was housed (the fifth or sixth). Each maxilla forms the lower edge of the external naris. A smooth channel commences at the anterior edge of the external naris, and extends forwards disappearing at the level of the fourth maxillary tooth. Ventrally, the mandibular rami almost cover the maxillae. However, it can be observed that the right maxilla starts at the external border of the internal naris. The exact number of alveoli is not known, because the left maxilla is preserved back to a point just anterior to the orbit, and the right one only half this distance (with 13 alveoli). Nevertheless, taking into account the extension of the

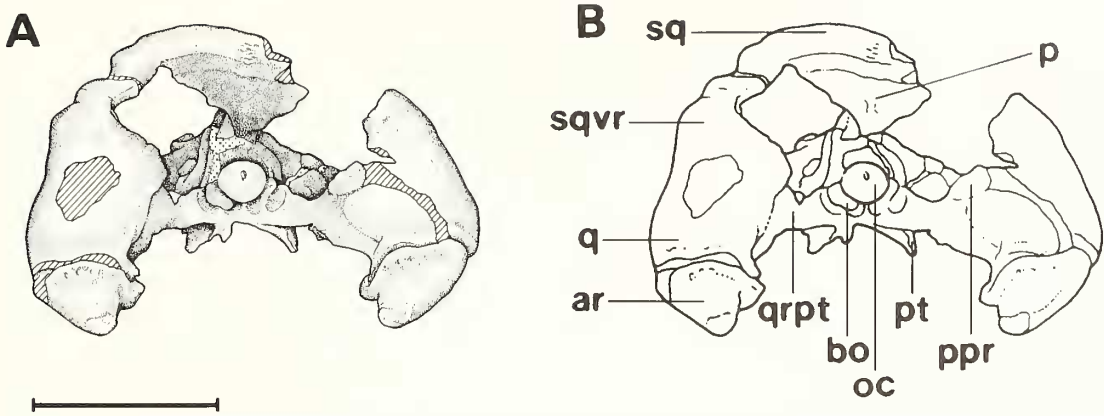
mandibular alveolar series, the maxillae had to extend up to the posterior part of the orbit, with approximately 22 alveoli for functional teeth.

Nares. The external nares are anterior to the orbits, level with seventh and ninth maxillary alveoli (in *R. thortoni*, BMNH R4853, the external nares are situated further anteriorly, as the anterior edge is by the fifth maxillary alveoli). They are oval, with the anterior-posterior diameter longer. Preservation effects have made their sizes different, the right one being longer than the left one. The nares are bordered by the premaxillae at the antero-superior edge and by the maxillae at the antero-inferior one (Text-fig. 2b). The posterior edge in both nares cannot be determined because of the lack of sutures in this area, but dorsally they are limited by the frontals, and on the right naris, a small fragment might belong to the prefrontal. The presence of lacrimals in plesiosaurs has been a matter of debate. Taylor (1992b, fig. 1) demarcated them with a dotted line in *R. zetlandicus*, while Storrs (1991) stated that the lacrimals were absent in most Sauropterygia, including plesiosaurs. However, lacrimals can be clearly observed in a new material of *Pliosaurus brachyspondylus* (Owen) (Taylor and Cruickshank 1993), or either may be fused to the maxilla as in *Rhomaleosaurus megacephalus* (Cruickshank 1994). In *Maresaurus* (MOZ 4386 V), there is a short suture line on the right side, which might coincide with the lacrimal anterior external edge. Furthermore, a channel which runs between the posterior external end of the naris and the anterior edge of the orbit, might belong to the lacrimal duct. Outside the naris, and over the maxilla (or lacrimal), there is a pair of large foramina (Text-figs 1b, 2b). No other known plesiosaur bears such foramina, so it is uncertain whether they are an autapomorphy of *Maresaurus coccai*, related to an osmoregulation mechanism (salt gland) or were produced by the fossilization process, that strangely left two almost symmetrical holes. Unfortunately, the lacrimal and prefrontal region in other pliosaurs with a spatulate symphysis is also either badly preserved or unknown. Furthermore, the problem of whether or not plesiosaurs possessed nasals is not resolved (Andrews 1913; Brown 1981; Storrs 1991; Taylor 1992b; Brown and Cruickshank 1994).

Parietal. If the parietal contacted the premaxillae, forming the interorbital bridge, it must have been narrow, ascending postero-dorsally after the contact. The pineal foramen, closed by a post-mortem break, would be placed in the parietal, just behind the postorbital arch. Although the back of the parietal is also eroded, a medial line can be observed, indicating that they were paired (at least internally, and probably visible in young specimens), in the narrower sector, in the anterior part of the bridge that divides the temporal fenestra. There is no interdigitated medial suture as in *R. zetlandicus* (Taylor 1992b, p. 251). Here, in lateral view, the parietal has an irregular structure with furrows and small anterior-posterior crests which serve as a union with the epipterygoid (Text-fig. 2A). Postero-dorsally, the parietal widens abruptly, it is markedly convex and ascends to the squamosals. A medial bump marks the end of what was a gentle crest of the parietal (Text-fig. 1b). As in *Rhomaleosaurus*, the parietal neither forms a narrow sagittal crest, nor reaches the posterior edge of the skull (Text-figs 1b, 2b). This does occur in *Simolestes* where a thin parietal bar is enclosed by the squamosals in the occipital edge of the skull. The posterior part of the parietal is covered by the squamosals so it can be observed in ventral and occipital view. It is a wide sub-triangular plate the vertex of which coincides with the sagittal line and is forwardly oriented. The ventral parietal plate has a medial crest and a pair of lateral shorter crests (Text-fig. 3).

Squamosals. The squamosals merge in the dorsal cranial roof, fusing with the parietals with a wide interdigitated suture. They form the highest part of the skull. The parietals do not extend under the anterodorsal crest of the squamosals as in *R. zetlandicus* (Taylor 1992b). Laterally, each squamosal forms the posterior edge of the temporal fenestra (the right fenestra is incomplete; Text-fig. 2A). This ramus is stout as in *Rhomaleosaurus*, while in *Simolestes* it is wider and more compressed. The dorsal rami are broken and the ventral ones are quite robust and are fused to the quadrates. Both dorsal surfaces are eroded and consequently the squamosal-quadrate suture is unclear; nor have the foramina been preserved, as in the *R. zetlandicus* holotype (Taylor 1992b). The ventral ramus is proportionately narrower than in *Simolestes*. As in *R. zetlandicus* and some plesiosauroids (Brown 1981; Taylor 1992b) the distal ramus of the paroccipital process is fixed to the medial face of the squamosal ventral ramus up to the quadrate suture.

Quadrate. The quadrate is massive and fused to the mandibular glenoid fossa (Text-fig. 3). It is covered dorsally by the descendent or ventral ramus of the squamosal, and laterally, in posterior and internal view, it surrounds the outer extremity of the paroccipital process. Internally, the quadrate covers dorsally the distal portion of the quadrate ramus of pterygoid. In that medial and posterior sector of the left quadrate there is a marked boss. On the right side, this boss is missing and represented by a hole. The quadrate condyles are partially broken



TEXT-FIG. 3. *Maresaurus coccai* gen. et sp. nov.; MOZ 4386 V; Lower Bajocian, Neuquén Basin, Argentina; occipital view. Scale bar represents 200 mm. For abbreviations see Appendix.

and as they are fused to the glenoid fossa, their morphology is not clear. They are wide but not very marked and both of them appear to end in slightly concave surfaces.

Epipterygoid. The epipterygoid has a wide base and lies dorsally on the parietal. Then it narrows into a stem or columella that runs downwards and fuses with the pterygoid anterior bar (Text-figs 1A, 2A). The left epipterygoid is somewhat displaced, but better preserved, and the quadrate ramus of pterygoid is fused to its posterior edge.

Palate. The palate of *Maresaurus* is closed (Text-figs 1C, 2C). Unlike those of *R. victor* and *R. zetlandicus*, it has no anterior interpalatal vacuity (Fraas 1910; Taylor 1992b). The tear-drop-shaped internal nares, are separated by the vomers, which are fused forming a convex bar. This bar continues forwards between the maxillae, which are almost covered by the mandibular rami. Behind the internal nares, the vomers widen and maintain a suture in the sagittal line, suggesting that they were paired, at least in the early ontogenetic developmental stages. Posteriorly the vomers make contact with the maxillae, palatines and pterygoids. The nares are bordered by vomers and maxillae; the palatines, as in *R. zetlandicus*, *R. victor* and *Simolestes vorax*, are not included. The flattened palatines merge outside the anterior rami of the pterygoids, reaching the anterior edge of a small suborbital fenestra elongated anterior-posteriorly and formed also by the external lateral and partially ventral ectopterygoid and the lateral ramus of the pterygoid. Both fenestrae are incomplete. The anterior edge of the subtemporal fenestra is beneath the limit formed by the ectopterygoid and the right pterygoid. Only the right ectopterygoid was preserved, partially superposed to the external margin of the palatine (Text-fig. 2C).

Pterygoids. The pterygoids are complete and run between the palatines, up to the seventh pair of maxillary alveoli, where they unite with the vomer and palatines with an interdigitated suture. The oblong interpterygoid vacuities, with the anterior-posterior diameter much longer, are in the posterior third of the pterygoid anterior rami. These vacuities have a slight separation in the posterior region, as in *R. zetlandicus*, and are partially divided by a projection of the parasphenoid. In *Simolestes*, the parasphenoid crest does not reach the posterior region of the vacuities (Andrews 1913, pl. 3), while in *Rhomaleosaurus* the parasphenoid is a full crested bar which separates both fossae. The parasphenoid runs in front of the interpterygoid vacuities and between the pterygoids, as in *Simolestes* (Andrews 1913), *R. megacephalus* (Cruickshank 1994) and probably in *R. zetlandicus* (Taylor 1992b). Laterally, and in front of the interpterygoid vacuities, the pterygoids expand and fuse with the ectopterygoids to form the posterior edge of the small vacuities mentioned above. The posterior part of the pterygoids is deeply concave due to the rise of the pterygoid boss (high posterior pterygoid wings). The pterygoid concavity is bigger and posteriorly more extended than in *R. victor*. In *Simolestes vorax* (holotype BMNH R3319) the pterygoid is flat. The pterygoids and their lateral long bars extend at both sides and below the palatine; posteriorly, they fuse to the anteromedial corner of the quadrate below the squamosal-quadrates contact. In the middle of their run they cover, in ventral view, the paroccipital processes.

Occipital region. The occipital region is incomplete (Text-fig. 3). The basioccipital forms the occipital condyle, which is slightly wider than high as in *R. zetlandicus* (Taylor 1992b), but shorter. As in *Rhomaleosaurus*, the condyle cannot be seen in dorsal aspect because it is covered by the squamosals. In *Simolestes* it is exposed. In the laterodorsal region of the condyle, on both sides of the neural canal, there are two depressed surfaces for the lost exoccipitals. On both sides of the condyle, the basioccipital has descending expansions (lateral processes of basioccipital of Andrews 1913, or basipterygoid process of Brown 1981) which lean on both hollows of the pterygoid posterior rami. The paraoccipital processes, both incomplete, are flat and rest on the pterygoid posterior rami, ending level with the squamosal-quadrato suture. On the left side, in front of the basioccipital, there are two bony elements. The ventral one may correspond to the basisphenoid (see *Kimmerosaurus langhami* Brown, 1981). The supraoccipital is not preserved.

Mandible. Both mandibular rami are preserved firmly attached to the skull and snout, and therefore the alveolar sector is partially covered by the premaxillae and maxillae. The mandibular symphysis is short and includes, in ventral view, six pairs of functional alveoli (it is important to define whether the number should be counted either from the ventral or the buccal view, since it can be different). The *Maresaurus* symphysis is wide (index: 0.97, considering the relationships between the symphysis maximum width over maximum length in ventral view), similar to that in *R. zetlandicus* (index: 1), but less than *Rhomaleosaurus victor* (index: 1.17), *Simolestes keileni* (index: 1.15) and *S. indicus* (index: 1.15) (Bardet *et al.* 1991; Godefroit 1994), and slightly wider than *S. vorax* (index: 0.86). The greater broadening of the symphysis in *Maresaurus coccai* is between the fifth and sixth alveoli, where it also rises in a similar degree to that of *R. cramptoni* (Carte and Baily 1863), greater than that of *R. zetlandicus* and less than in *R. victor* and the holotype of *Simolestes vorax* (in BMNH R3170 it is dorsally flattened). The snout does not cover the mandibular symphysis as in *R. victor*. Instead, in *R. cramptoni*, according to Carte and Baily (1863 pl. 7, fig. 1), it covers the symphysis. The mandibular symphysis of *Maresaurus* narrows forwards and ends rounded, with only one pair of small alveoli; behind the sixth pair of alveoli the symphysis narrows abruptly and then separates into both mandibular rami. The splenials can be observed in ventral view, being part of the symphysis, level with the fourth pair of alveoli. The lateral and ventral walls of the symphysis have deep anterolaterally orientated holes and numerous foramina, those parallel to the alveolar edge coinciding with each interalveolar septum. Between the seventh and tenth alveoli, the dentary narrows where the vertical walls are the lower ones. Then, it separates and deepens until it reaches the coronoid eminence. The dentary has 24 alveoli. In medial view it is fused to the splenial and ventrally the angular reaches it at the tenth alveolus level. Posteriorly, it contacts the surangular, although the suture is not preserved (Text-fig. 2A).

The coronoid is exposed on the inner face of the mandible; the coronoid eminence is not conspicuous and appears behind the most posterior alveoli, while the maxilla covers it externally. In medial view, the coronoid contacts anteriorly with the splenial and posteriorly with the surangular above, and the prearticular below. The prearticular is long, since it extends from the intermandibular foramen probably up to the articular, but there are no sutures that prove whether the prearticular was part of the glenoid fossae anterior wall. The prearticular has been identified both in pliosauroids (*R. zetlandicus*; Taylor 1992b) and in plesiosaurids (*Alzadasaurus colombianus* Welles, 1962). The angular is another long element that extends ventrally and laterally to the tenth alveolus. Externally, it forms the expanded base of the adductor fossa, incised mainly in the surangular, and serves as support for the articular (glenoid fossa).

In front of the glenoid zone there are no sutures demarcating the bones. Consequently it is impossible to know whether this region was bordered by part of the surangular and the prearticular or only by the articular, and the extent of participation, if any, of the angular in the retroarticular process. The retroarticular processes are dorsally trapezoidal, with flat surface (Text-figs 1B, 3). However, their bodies are high and ventrally convex (Text-fig. 1A). These retroarticular processes are like those of *R. zetlandicus*, but differ from those of *R. victor* which are compressed and high, and are very different from those of *Simolestes vorax* which are flat. Though the retroarticular processes of *S. keileni* are damaged, their proportions are similar to those of *Maresaurus* and different from those of *Simolestes vorax*.

Dentition

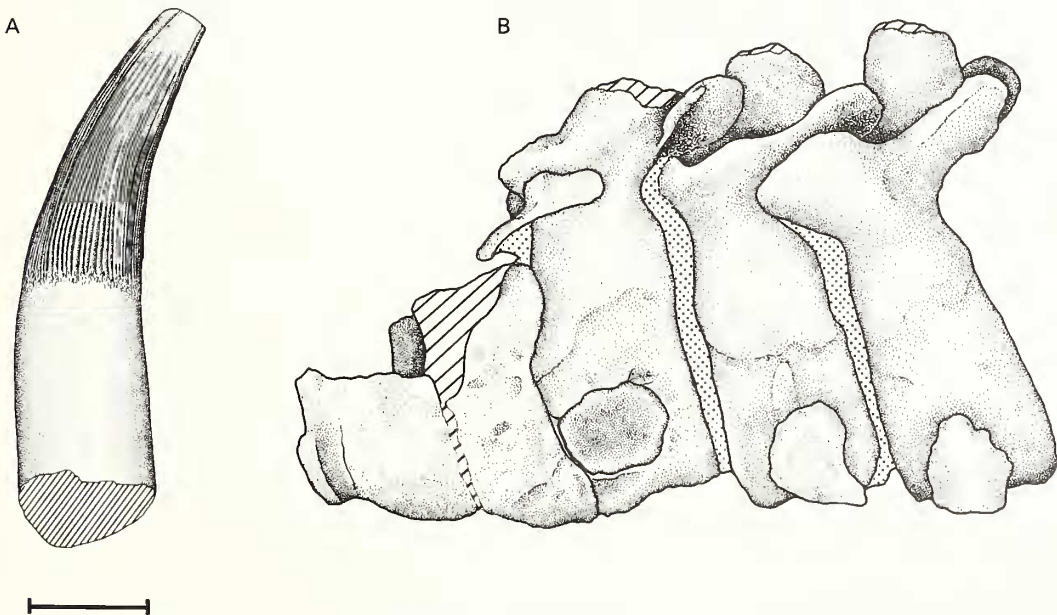
Each premaxilla bears five alveoli for functional teeth. The first is small and medial, the second is twice as large, and the third, fourth and fifth held hypertrophied teeth (caniniform *sensu* Tarlo 1960). Posteriorly, there is a large interalveolar space which corresponds to the premaxilla-maxilla union. The hypertrophied sixth mandibular tooth fitted into this space. The first alveolus of the maxilla is small, the second is slightly larger, the third, fourth and fifth are hypertrophied, especially the fourth, which coincides with the maxillary wave

maximum inflexion. From the sixth alveolus posteriorly, they decrease in size. Both maxillary rami are incomplete; the right one bears 19 alveoli and the left one 14. However, considering the jaw dental series, the maxillary teeth may have numbered 24. The dentaries retain the entire alveolar line (25 in the left side and 24+ on the right side) and several tooth remains in different developmental stages. The mandibular symphysis bears in ventral view, six pairs of alveoli, the first of which is small, the second and third, bigger, and the fourth to sixth, hypertrophied. From the seventh pair of alveoli, there is a narrowing with reduction of the alveoli, coincident with the separation of the mandibular rami. Posterior to the eighth pair of alveoli, there is a wide interalveolar space, visible in the left dentary, where the third maxillary hypertrophied tooth was housed. This is not seen in *Rhomaleosaurus*, where there are no spaces or diastemas. Finally, the series ends with 13 medium-sized alveoli of which the last three are the smallest. All the alveoli are circular to sub-circular, in accordance with the cross section of the functional teeth. In the rear of the left mandibular ramus, several small alveoli are preserved which correspond to replacement teeth. As in all plesiosaurs, these replacement teeth are placed medially and posteriorly to the alveoli of the functional teeth. Based on the opening or occlusion degree of these small alveoli, there appears to have been alternate tooth replacement in waves, from back to front (Edmund 1960).

Several teeth were detached during the excavation. The most complete is a hypertrophied one (Text-fig. 4A), circular in cross section, backwardly recurved, with an incomplete root without carinae, striated crown and the apex with only four striae. The striae are not dichotomously branching; they have a compact distribution (20 striae per 10 mm in the middle of the crown), and the pattern is of one (occasionally two to three) shorter stria between longer ones, of which only four reach the smooth apex. One pair of long striae is situated on the lateral face of the crown and the other pair on the inner face. In spite of being hypertrophied, this tooth has no smooth faces as in *Rhomaleosaurus zetlandicus*, *R. cramptoni*, *Simolestes keileni* and *S. vorax*. As in all pre-Kimmeridgian pliosaurids, all the teeth cross sections of *Maresaurus* are circular. The Kimmeridgian-Tithonian specimens have triangular sections (Tarlo 1960).

Vertebrae

The atlas, axis and three articulated anterior cervical vertebrae are the only postcranial skeletal elements preserved (Text-fig. 4B), together with two other cervical vertebrae, also from the anterior sector of the neck. The atlas and axis are fused by their lateral faces, but not ventrally, where they are separated by a deep furrow.



TEXT-FIG. 4. *Maresaurus coccai* gen. et sp. nov.; MOZ 4386 V; Lower Bajocian, Neuquén Basin, Argentina. A, caniniform tooth. B, atlas-axis and cervical vertebrae. Scale bar represents 20 mm (A), 30 mm (B).

The anterior part of the atlas body is deeply concave. Laterally the atlas body is longer than the axis and there is a ventrolateral furrow which forms a 'lip' surrounding the occipital condyle. The left side of the atlas-axis is more damaged, but the right side preserves part of a long post-zygapophysis which reaches the first cervical vertebra. The three following cervical vertebrae are short, wider than long. In the first one, the rib is detached and it can be observed that the hollow remaining, belonging to the synapophysis is not divided; so, at this level of the neck, the ribs were unicipital. The two isolated vertebrae, which also belong to the anterior sector of the neck, show a small narrowing in the synapophysis, suggesting that the ribs there were bicipital. Both *Rhomaleosaurus thorntoni* and *R. cramptoni* have cervical vertebrae with a divided synapophysis. In both cases, the cervicals were not the more anterior ones (Carte and Baily 1863; Andrews 1922). The neural spine is low and strong in the more anterior cervicals and higher in the following ones. The pre- and post-zygapophyses are wide and low.

DISCUSSION

Phylogenetic analysis of sauropterygians has advanced significantly in recent years (Rieppel 1989; Sues 1989; Storrs 1991). However, according to Taylor and Cruickshank (1993), the inter-relationships between sauropterygians and plesiosaurs need defining with more precision, and important progress depends on the study of more Jurassic plesiosaurs. Brown (1981) made a significant contribution, carrying out a detailed analysis of plesiosaur characters. He selected some synapomorphies used to discriminate families, and removed other characters as either plesiomorphic or subject to ontogenetic variation. However, it is difficult to distinguish synapomorphies in Jurassic pliosaurids working only with skulls, because of the possibility that similarities could either be due to close phylogenetic links or convergences in response to similar feeding habits. Furthermore, there have been few studies on Jurassic pliosaurids with relatively complete skulls. The classic studies of Andrews (1913, 1922) were followed by the recent and outstanding reviews of Taylor (1992a, 1992b), Taylor and Cruickshank (1993) and Cruickshank (1994).

Pliosaurids are considered to be the sister-group of plesiosauroids because of their cheek structure (Brown and Cruickshank 1994). All Liassic pliosaurids are mesorostral (rostrum length, from the premaxilla to the orbit anterior edge/skull length, from the premaxilla to the squamosal: < 0.50). The mesorostry is shared by *Rhomaleosaurus*, *Maresaurus* and *Simolestes*, while *Peloneustes*, *Liopleurodon* and some species of *Pliosaurus* share the long rostrum (index > 0.50) as a derived character. However, the spatulate symphysis shared by *Rhomaleosaurus*, *Maresaurus* and *Simolestes* could be a convergent character of animals with similar feeding habits. So, at present, there is no synapomorphy known to support the monophyly of the spatulate genera, and in this sense, in agreement with Brown (1981), Rhomaleosauridae is considered not to be a valid taxon. *Maresaurus* and *Rhomaleosaurus* share: the parietal not reaching the occipital edge of the cranial plate and not forming the sagittal crest between the squamosals (probably a primitive character which is maintained in *Pliosaurus*); the occipital condyle not visible in dorsal view; and the squamosal dorsal ramus with elliptical cross section. In *Simolestes*, the parietal is a crest that reaches the posterior edge of the skull, the occipital condyle is visible in dorsal view, and the squamosal dorsal ramus is compressed and sub-triangular in cross section. *Maresaurus* shares with *Simolestes* (and *Liopleurodon*) derived characters such as the lack of dorso-medial foramen, the lack of anterior interpterygoid vacuity (both present in *Rhomaleosaurus* and *Pliosaurus*) and fewer than 26 alveoli in the dentary (Liassic pliosaurids and some species of *Pliosaurus* have at least 30). Among Jurassic pliosaurids, *Rhomaleosaurus* is probably the most primitive, and *Simolestes*, the most derived. *Maresaurus* shares characters with both. However, *Maresaurus* has autapomorphies which justify its differentiation at generic and specific level: the strong flanges formed by the pmx-mx; the parasphenoid that does not separate completely the interpterygoid vacuities; the expanded and elevated pterygoid wings; the hypertrophied teeth densely striated without carines and smooth faces; and a diastem between the eighth and ninth mandibular alveoli. If those foramina placed externally to the external nares are not artefacts, this is another autapomorphy of *Maresaurus*. In order to understand the phylogeny of *Maresaurus*, it is necessary to approach the revision of all the Jurassic pliosaurids using the same taxonomic criteria.

Records of Bajocian marine reptiles are scarce world-wide (Bardet 1992; Gasparini 1992; Gasparini and Fernández 1996). Even scarcer are records of plesiosaurs, which are restricted to *Simolestes keileni* from the Upper Bajocian of France (Godefroit 1994) and *Maresaurus coccai* from the Lower Bajocian of the Neuquén Basin. The extinction of the rich Early Jurassic marine reptile fauna in the European Tethys may have been a response to the shallowing of the basins. When lagoons prevailed, thalattosuchians were almost exclusive in the pre-Callovian marine herpetofauna (Bardet 1992; Vignaud 1995; Mazin *et al.* in press). On the contrary, the assemblage of marine reptiles in the Lower Bajocian in the Neuquén Basin comprises pelagic and off-shore forms, namely pliosaurids, at least two taxa of large ichthyosaurs, and a large thalattosuchian (Fernández 1994; Spalletti *et al.* 1994). Accordingly, the palaeoenvironment is interpreted as an off-shore deposit dominated by pelagic sedimentation (Spalletti *et al.* 1994); and in the *Emileia giebeli* zone, where the marine reptiles were discovered, bivalves, brachiopods, ammonoids and microfossils attained high diversity (Riccardi *et al.* 1994).

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APPENDIX: LIST OF ABBREVIATIONS

a	angular	piv	posterior interpterygoid vacuities
adc	anterodorsal crest	pal	palatine
ar	articular	pmx	premaxilla
arpt	anterior ramus of pterygoid	ppr	paroccipital process
bo	basioccipital	prf	prefrontal
c	coronoid	ps	parasphenoid
d	dentary	pt	pterygoid
ec	ectopterygoid	q	quadrate
en	external naris	qrpt	quadrate ramus of pterygoid
ep	epipterygoid	sa	surangular
fr	frontal	sp	splenial
ho	hole	sof	suborbital fenestra
in	internal naris	sq	squamosal
mx	maxilla	sqv	squamosal ventral rami
no	notch	stf	subtemporal fenestra
oc	occipital condyle	tf	temporal fenestra
p	parietal	v	vomer
pa	prearticular		